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Comparisons of populations of oats (*Avena sativa* L.) developed by intra- and interspecific hybridization

by

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INTRODUCTION

The hexaploid Avena species, A. sterilis L., A. fatua L., A. sativa L., and A. byzantina C. Koch, belong to a single biological species and comprise the primary gene pool of the cultivated oat (A. sativa). The hexaploids are interfertile, exhibit regular bivalent pairing, and have the A, C, and D genomes (Rajhathy and Thomas, 1974). The aggressive, adaptable, weedy, and typically Mediterranean A. sterilis is the progenitor of all hexaploid oats, having greater diversity than the other spontaneous subspecies A. fatua (Coffman, 1977). Avena fatua is a specialized weed associated with cultivation; therefore, the probability of germplasm exchange between the cultivated and A. fatua gene pools has been greater than between the cultivated and more geographically isolated A. sterilis gene pools.

Landrace cultivars introduced into the spring oat growing areas of North America were predominantly European A. sativa cultivars. In the Upper Mississippi Valley, two heterogeneous varietal introductions, 'Kherson' and 'Green Russian', were the primary source of improved cultivars during the first one-third of this century (Coffman, 1977). An abrupt grain yield increase during the period 1932-1942, following the introduction of A. byzantina germplasm into A. sativa breeding populations, suggested that the original introductions had limited genetic variability for grain yield (Langer

et al., 1978). Avena sativa and A. byzantina represent the northern and southern European gene pools of the cultivated oat. Similarly, introgression of A. sterilis germplasm into the midwestern A. sativa gene pool has produced agronomically desirable lines from backcross breeding with grain yields of up to 30% above the recurrent parent (Frey and Browning, 1971; Lawrence and Frey, 1976; Frey, 1976).

Although A. sterilis germplasm is a source of new yield genes, the rapidity with which this new source of variability will be exploited depends on the amount of genetic variability presently available to the breeder. Considerable progress in grain yielding ability has been achieved during the past decade by utilizing adapted and exotic germplasm from within the North American cultivated oat gene pool.

This study was designed to compare characteristics of six oat populations developed by interspecific (A. sterilis x A. sativa) and intraspecific (A. sativa x A. sativa) hybridizations that would indicate their potential utility in an oat breeding program. Four interspecific populations with a mean of 12.5% A. sterilis and 87.5% A. sativa germplasms were compared with two intraspecific populations developed by intercrossing superior A. sativa cultivars.

LITERATURE REVIEW

Reduced genetic variability within the cultivated gene pools of crop species is a phenomenon of contemporary agricultural systems. In extreme circumstances, this reduction can suspend progress from selection or precipitate catastrophies such as the Irish potato famine (Salaman, 1949). Consequently, the introgression of germplasm from exotic, wild, or weedy relatives is an integral part of many plant breeding programs (Harlan, 1976; Hawkes, 1977). In the broadest sense, introgressive hybridization is the incorporation of germplasm from one isolated population into another of the same or a related species (Heiser, 1973). It is believed to play an evolutionary role, and introgression between sympatric domesticated plants and their wild relatives is common (Stebbins, 1959; Anderson, 1961; Heiser, 1973).

Maize

Cultivated maize (Zea mays L.) is the product of repeated racial hybridization within the species and recurrent introgression from teosinte (Z. mexicana) and Tripsacum (Mangelsdorf, 1961). Anderson and Brown (1952) considered the hybrids between the Southern Dent and Northern Flint maizes diverse enough to be interspecific and suggested a reexamination of these races to create maximum heterozygosity.

Griffing and Lindstrom (1954) and Moll et al., (1962,

1965) concluded that heterosis was associated with genetic diversity in crosses between North American and Central and South American germplasms. Griffing and Lindstrom (1954) suggested selecting genetically divergent parental material with the minimum divergence from agronomic standards. Moll et al. (1962) found the greatest heterosis and grain yield in hybrids between Puerto Rican and southeastern U.S. varieties, but an increase in genetic diversity beyond the Puerto Rican-U.S. level resulted in a decline in heterosis and grain yield (Moll et al., 1965). In a comparison of the Corn Belt Composite and a composite of the same material crossed to West Indian varieties, genetic variance for grain yield, expected gain from selection, and the upper range for full-sib family means were greater for the West Indian Composite (Goodman, 1965). Eberhart (1971), Hallauer (1972), and Hallauer and Sears (1972) reported that synthetic varieties with exotic germplasm could contribute to Corn Belt breeding programs. Conversely, Kramer and Ullstrup (1959) evaluated a large number of introductions in testcrosses and found a strong association between grain yield and maturity.

Mangelsdorf (1961) attributed heat and drought tolerance and some disease and insect resistance to teosinte introgression. Reeves (1950) introgressed Florida teosinte into two Texas inbreds and found increased heat tolerance and grain yield in the modified lines. Mangelsdorf (1952)

believed the introgression involved chromosome segments with multiple effects that represent definite genetic entities, and Sehgal and Brown (1965) suggested that populations of maize had become established with certain blocks of teosinte genes substituted for their homologues from maize. Lambert and Leng (1965) found increases in kernel row number and grain weight over four backcross generations in maize-teosinte populations, and differences between populations were related to the geographical origins of the strains of teosinte. Efron and Everett (1969) found synthetics with teosinte germplasm were earlier maturing, vegetatively less vigorous, but had higher percentages of dry matter in grain and stover.

The more alien cytogenetic nature of Tripsacum germplasm makes its incorporation into corn extremely complex (Galinat, 1977). Reeves and Bockholt (1964) recovered few fertile plants after backcrossing a Texas inbred onto T. dactyloides, but the modified inbreds had improved grain yields and less top firing and chlorophyll breakdown. Exchange between tetraploid T. dactyloides and maize chromosomes utilizing a stable triploid hybrid has been reported (Engle et al., 1973), but Harlan (1976) failed to recover the corn phenotype after ten backcrosses of a maize-Tripsacum hybrid to maize.

Soybeans

NAS (1972) observed that most soybean [*Glycine max* (L.) Merrill] varieties grown in the United States were related to only 11 introductions, so the introgression of exotic germplasm into breeding populations of this species would be timely.

Homozygous lines from soybean populations with 25% exotic germplasm (adapted x exotic 2x adapted) generally had higher mean grain yields, protein, oil, and protein + oil than lines from populations with 50% exotic germplasm (adapted x exotic) (Thorne and Fehr, 1970a, b). Generally, population rankings were predictable based on parental performance excepting grain yield in 3-way populations, and additive effects were more important than epistatic effects. Genetic variances were larger in 3-way than 2-way populations for grain yield, but genetic variances, heritabilities, and correlations among traits were similar in both population sets for protein. They concluded that exotic germplasm was a useful source of variability for protein + oil and 3-way populations were superior to 2-way populations for selecting high-yielding lines.

Schoener and Fehr (1979) tested lines from populations with 0-100% unadapted germplasm which had undergone up to five generations of intermating. The greatest frequency of high-yielding lines came from populations with the lowest

amount of exotic germplasm, but the highest yielding line came from a population with 75% unadapted germplasm. Populations with 25-75% unadapted germplasm had the largest genetic variances. They concluded that, for long-term breeding programs, populations with up to 50% exotic germplasm could be utilized provided the exotic parent displayed reasonable agronomic performance.

Sorghum

Early sorghum [Sorghum bicolor (L.) Moench] improvement in the U.S. was based on kafir x milo and kafir x feterita crosses, and more recently, kafirs from South Africa crossed with milos from North Africa have provided the male sterility and restorer genes that made hybrid sorghum production feasible (Doggett, 1976).

The sorghum conversion program is designed to change unadapted tropical sorghums to shorter, earlier, day-neutral types for direct use in temperate areas (Stephens et al., 1967; Webster, 1975). This program facilitates the large-scale introgression of germplasm for grain yield, insect and disease resistance, and nutritional quality into North American breeding programs.

In a diallel cross of exotic and adapted parents, F_1 hybrids involving exotics had the highest grain yields and GCA effects (Niehaus and Pickett, 1966). Nevertheless, they

concluded that the effects of general genetic diversity were confounded with the effects of heterozygosity for a relatively few height and maturity genes. Malm (1968) found substantial heterosis for grain yield and protein in hybrids between common male sterile lines and restorer lines developed from African introductions. Sixteen of 32 hybrids involving exotic lines yielded more than the best check, and GCA effects were larger than SCA effects for yield and seed size. He concluded that genetic diversity was the key to hybrid vigor. Laosuwan and Atkins (1977), using 11 converted lines crossed to testers in Iowa, found heterosis and heterobeltiosis levels well above those reported in studies using adapted lines. GCA effects of the converted lines were larger than SCA effects and they recommended preliminary screening of converted lines using testcrosses.

Rice

Heterosis for plant height, tillering ability, and single plant yield was observed in an indica-japonica (Oryza sativa L.) hybridization program in Asia in the late 1940s (Parthasarathy, 1972). The objective was to combine the characteristics of both groups, but success was limited, possibly due to the japonica parents and selection methods utilized. Hybrids of indicas with varieties of intermediate type and good fertilizer responsiveness were also unsuccessful.

Parthasarathy (1972) noted that isolated ecotypes from upland regions were sources of genetic variability for many traits and breeders in the U.S. produced high yielding indicas from crosses with upland japonicas from the Philippines and Taiwan. Ponlai varieties developed in Taiwan during 1931-1943 had exotic parents and, recently, introductions with resistance to fungal and insect pests were backcrossed onto short-statured indica varieties (Huang et al., 1972). In Japan, the genetic base has been broadened through the use of exotics to improve heading behavior, panicle type, plant vigor, and disease and stress resistance (Okabe, 1972). The International Rice Research Institute has used tropical indicas as sources of dwarfing genes, vegetative vigor, and tillering ability, and japonicas and U.S. varieties for glaborous plant parts, disease resistance, cold tolerance, tough leaves, slow senescence, grain shape, appearance, and cooking quality (Beachell et al., 1972). Oryza nivara from India contributed virus resistance and a bulu variety from Indonesia the nonshattering trait. Generally, rice breeding today involves hybridizations between tropical and temperate groups (Poehlman, 1979).

Wheat

Many of the interspecific and intergeneric crosses in wheat (Triticum spp) used novel cytological manipulations to

facilitate the incorporation of qualitative rather than quantitative characters (Sears, 1956; Riley et al., 1968; Kimber, 1967; Dosba and Doussinault, 1973). Nevertheless, Carlson et al. (1978) transferred insect resistance from T. turgidum to T. aestivum by backcrossing, and Shands (1941) recovered fertile progeny from T. timopheevii-T. vulgare crosses that carried disease resistance genes from T. timopheevii. Wheat stem rust (Puccinia graminis tritici) resistance has been transferred from T. durum to T. vulgare by selecting in segregating generations for the hexaploid phenotype (Hayes et al., 1920; Goulden, 1929; Peterson and Love, 1940).

Smith (1942) reported that Triticum-Agropyron hybrids were sterile, but Knott (1961, 1964) found no detrimental effects from the substitution of an Agropyron chromosome carrying leaf rust (Puccinia recondita tritici) resistance for chromosome 6A of the hexaploid 'Thatcher'. Wienhues (1966) reported decreased vigor, but good grain development, in T. aestivum backcross lines with Agropyron addition chromosomes. Riley and Chapman (1958) added rye chromosome pairs to the hexploid wheat complement and found distinctive modifications to the phenotype of quantitative traits.

F_1 hybrids between spring and winter wheats were found to outyield the spring parents by up to 40% (Grant and McKenzie, 1970) and CIMMYT (1979) described a program to

combine the separate winter and spring wheat gene pools to upgrade grain yield, disease resistance, drought and cold tolerance and increase the range of maturity in both types.

Oats

Williams (1969) found genetic variances and high yield segregates associated with parental diversity in crosses of adapted and unadapted (predominantly A. sativa) parents. Cross means were frequently inferior to midparent values in single crosses, but 3-way (adapted x exotic 2x adapted) crosses were more predictable, possibly due to the restoration of favorable epistatic combinations.

In experiments conducted in crown rust (Puccinia coronata Cda.)-free environments, Frey and Browning (1971) and Frey (1972) found significant deviations in grain yields associated with rust resistance genes transferred from A. sterilis into two A. sativa backgrounds. Jondle (1974) reported that deviations associated with rust resistance could be transferred to other recurrent parents by backcrossing, and the segregation pattern in resistant and susceptible isopopulations indicated linkage rather than pleiotropism between grain yield and rust resistance loci.

No sterility or cross-incompatabilities were found in hybrids between A. sativa and A. sterilis, but meiotic irregularities in the form of univalent, trivalent, and

quadrivalent associations between chromosomes were frequent (Rezai, 1976). He indicated that multivalent formations could cause irregular segregation.

Campbell and Frey (1972) and Cox (1979) found transgressive segregates for high groat protein percentage in combinations of A. sativa and A. sterilis germplasms. Additive effects were most important, but epistatic effects were present in some crosses.

A further set of A. sterilis x A. sativa backcross populations produced large amounts of genetic variability for grain yield, and high-yielding transgressive segregates were most frequent in the Bc_1F_2 to Bc_4F_2 generations (Lawrence and Frey, 1975). Grain yield was controlled by genes exhibiting additive, epistatic, and linkage effects with one-third of the plus factors for grain yield coming from the A. sterilis parents (Lawrence and Frey, 1976). Several backcross lines with acceptable agronomic quality outyielded the recurrent parents by up to 30% (Frey, 1976). One backcross population exhibited transgressive segregation for oil percentage and this trait was not correlated with groat weight, heading date, or plant height (Frey et al., 1975). Over 90% of the grain yield variation in these interspecific matings was accounted for by growth rate and harvest index (Takeda and Frey, 1976), and by the Bc_5 generation the relative contribution of growth rate to grain yield was 1.5 times that of

harvest index. More specifically, Helsel and Frey (1978) postulated that an increase in the size and duration of the photosynthetic system in some high-yielding lines relative to their recurrent parent resulted in an increased number of spikelets per panicle and kernel weight. Moreover, this was accomplished without changes in maturity or heading date.

A further set of interspecific isopopulations, distinguished by their cytoplasms, showed significant positive effects for grain yield, heading date, straw yield, plant height, growth rate, and harvest index due to A. sterilis cytoplasm (Robertson, 1980). However, the effects on straw yield, plant height, and growth rate decreased with backcrossing. Over all interspecific matings, Bc_2F_2-derived lines with A. sterilis cytoplasm had a grain yield advantage of 5.3%.

MATERIALS AND METHODS

Development of Material

The six populations evaluated in this study (Table 1) consisted of four developed by interspecific hybridization (symbol "W" denotes presence of wild A. sterilis germplasm) and two developed by intraspecific hybridization (symbol "C" denotes presence of only cultivated A. sativa germplasm).

The four A. sterilis plant introductions (PI), from Israel, were spring or facultative types selected at random. The six A. sativa parents, 'Otter' (CI 8304), 'Grundy' (CI 8445), 'Noble' (CI 9194), 'Lang' (CI 9257), 'Wright' (CI 9218), and 'Chief' (CI 9081), were popular spring-oat cultivars of superior agronomic quality and typical of material selected to initiate a cultivar development program. They also represented a diverse sample of germplasm as the majority of progeny from single-crosses among the cultivars had less than 15% of their genes identical by descent (Table 2).

The A. sterilis introductions served as the pollen parents for the initial cross in the development of W1 and W2; conversely, the A. sativa cultivar, Otter, served as the pollen parent for the initial cross in W3 and W4 (Table 1). These cytoplasmic differences were maintained in subsequent backcross generations; thus, lines in W1 and W2 had A. sativa

Table 1. The pedigree, symbol, and number of F_2-derived lines representing each of the six oat populations

Population[a]	Pedigree	Number of lines evaluated
W1	Otter x PI 317789 2x Grundy 3x Noble	512
W2	Otter x PI 317973 2x Grundy 3x Noble	512
W3	PI 317989 x Otter 2x Grundy 3x Noble	512
W4	PI 318016 x Otter 2x Grundy 3x Noble	512
C1	All three 3-way cross combinations among Otter, Grundy, and Noble	510
C2	All three single-cross combinations among Otter, Grundy, and Noble each crossed to Lang, Wright, and Chief	576

[a]W denotes a population developed by interspecific hybridization; C denotes a population developed by intraspecific hybridization.

Table 2. Inbreeding coefficients of F_1 progeny from single-crosses among the six A. sativa cultivars

	Grundy	Noble	Lang	Wright	Chief
Otter	0.11	0.07	0.09	0.05	0.10
Grundy		0.28	0.31	0.09	0.44
Noble			0.28	0.08	0.41
Lang				0.06	0.33
Wright					0.13

cytoplasm and lines in W3 and W4 had A. sterilis cytoplasm. To construct each W population, Noble was crossed to 8 Bc_1F_1 plants and 8 Bc_2F_1 seeds were produced on each Bc_1F_1 plant. These were advanced one generation in the greenhouse in spring 1976, and the 64 Bc_2F_2 bulks were propagated in the field in 1977. Mild selection was practiced against shattering types and in 1979 eight spaced plants representing each bulk were grown in the field along with the parental lines. These plants were threshed separately to produce the 512 F_3-derived lines (i.e., 8 lines in each of 64 Bc_2F_1 families) in each population. The lines in these populations were expected to contain 87.5% A. sativa and 12.5% A. sterilis germplasms.

To construct C1, 13 F_1 seeds from each of the three 3-way crosses among Otter, Grundy, and Noble were advanced to the F_3 generation in the greenhouse in 1978. Thirteen spaced plants per F_3 bulk, plus three chosen at random, grown in the field in 1979, were threshed separately to produce the 510 F_3-derived lines (i.e., 13 lines in each of 13 F_1 families from each of three 3-way crosses plus three random lines) in this population. Each cultivar contributed equally to the overall population. In three instances, all 13 spaced plants representing an F_3 bulk did not produce sufficient seed for evaluation in six replicates. Consequently, lines were selected at random from other F_1 families representing the same

3-way cross in order to preserve the overall symmetry of the population.

To construct C2, each of the three single-cross combinations among Otter, Grundy, and Noble were crossed with Lang, Wright, and Chief, giving nine 3-way cross combinations. Eight F_1 seeds per combination were advanced to the F_3 generation in the greenhouse in 1978 and eight spaced plants per bulk plus parents were grown in the field in 1979. These plants were threshed separately to produce the 576 F_3-derived lines (i.e., 8 lines in each of 8 F_1 families from each of 9 crosses) in this population. Each cultivar contributed equally to the overall population. Again, sufficient seed for evaluation was not obtained in three instances and random lines were selected as in C1.

Field Evaluation

The six populations were evaluated using F_3-derived lines in the F_4 in a randomized complete block experiment with six replicates in 1980. Two replicates were grown at the Agronomy Field Research Center (AFRC) west of Ames, Iowa on a soil of the Clarion-Webster association, two were grown under irrigation at the Hinds Farm, north of Ames, Iowa, on a Coland loam soil type, and two were grown at Kanawha, northcentral Iowa, on a soil of the Clarion-Nicollet-Webster association. Sowing dates were April 7, April 11, and April 19 for the three

locations, respectively. A plot was a hill sown with 31 seeds and hills were spaced 30 cm apart in perpendicular directions. Plots were hand weeded and foliar diseases were controlled by periodic spraying between anthesis and maturity with the fungicide Maneb. A total of 23 cm of water was applied at the Hinds Farm over five dates between 24 April and 11 May.

The following traits were measured on a per plot basis:

Heading date (HD): Number of days after planting on which 50% of the panicles had fully emerged from the leaf sheaths. Measured on two replicates at the AFRC and one at the Hinds Farm.

Plant height (HT): Distance (cm) from ground level to tips of panicles two weeks post anthesis. Measured on same replicates as heading date.

Bundle weight (BWT): Dry weight (q/ha) of total above-ground plant material. Measured on six replicates.

Grain yield (GYD): Dry weight (q/ha) of threshed grain. Measured on six replicates.

Straw yield (SYD): Bundle weight minus grain yield (q/ha). Measured on six replicates.

Harvest index (HI): Grain yield expressed as a percentage of bundle weight. Measured on six replicates.

Growth rate (GR): Straw yield divided by heading date (q/da/ha). Measured on same replicates as heading date.

Statistical Analysis

A combined analysis of variance across locations was computed for the traits GYD, SYD, and HI for each population using the following model:

$$Y_{ijk} = M + L_i + R_{ij} + G_k + (LG)_{ik} + E_{ijk} \quad ,$$

and for the traits HD, HT, and GR, measured on three replicates, the following model was used:

$$Y_{jk} = M + R_j + G_k + E_{jk} \quad ,$$

where:

Y_{ijk} = GYD, SYD, or HI of the kth line in the jth replicate in the ith location,

Y_{jk} = HD, HT, or GR of the kth line in the jth replicate,

M = overall mean,

L_i = the effect of the ith location,

R_{ij} = the effect of the jth replicate in the ith location,

R_j = the effect of the jth replicate,

G_k = the effect of the kth line,

E_{ijk} and E_{jk} = residual variation,

and the term in parentheses represents an interaction of main effects.

Subsequent partitioning of the variances among lines in the interspecific populations into sources due to backcross

families and their interactions in combined analyses of variance for the traits GYD, SYD, and HI were conducted using the following model:

$$Y_{ijlmk} = M + L_i + R_{ij} + BCO_l + BCT_{lm} + GWBT_{lmk} + (LBCO)_{il} + (LBCT)_{ilm} + (LGWBT)_{ilmk} + E_{ijlmk} ,$$

and for the traits GR, HT and HD, the following model was used:

$$Y_{jlmk} = M + R_j + BCO_l + BCT_{lm} + GWBT_{lmk} + E_{jlmk} ,$$

where:

Y_{ijlmk} = GYD, SYD, or HI of the kth line in the mth Bc_2 family in the lth Bc_1 family grown in the jth replicate at the ith location,

Y_{jlmk} = GR, HT, or HD of the kth line in the mth Bc_2 family in the lth Bc_1 family grown in the jth replicate,

BCO_l = the effect of the lth Bc_1 family,

BCT_{lm} = the effect of the mth Bc_2 family in the lth Bc_1 family,

$GWBT_{lmk}$ = the effect of the kth line in the mth Bc_2 family in the lth Bc_1 family,

E_{ijlmk} and E_{jlmk} = residual variation.

All main effects were considered random in the calculation of variance components from expected mean squares, which are detailed in Table 3 for a combined analysis of a W population

Table 3. The sources of variation, degrees of freedom, and expected mean squares in a combined analysis of a W population

Source of variation[a]	Degrees of freedom[b]	
Loc	$(\ell-1)$	
Rep/Loc	$\ell(r-1)$	
Gen	$(G-1)$	$\sigma^2_e + r\sigma^2_{G\ell} + r\ell\sigma^2_G$
BC_1	(b_1-1)	$\sigma^2_e + r\sigma^2_{g/b_2/b_1\ell} +$
BC_2/BC_1	$b_1(b_2-1)$	$\sigma^2_e + r\sigma^2_{g/b_2/b_1\ell} +$
$Gen/BC_2/BC_1$	$b_1b_2(g-1)$	$\sigma^2_e + r\sigma^2_{g/b_2/b_1\ell} +$
Gen x Loc	$(G-1)(\ell-1)$	$\sigma^2_e + r\sigma^2_{G\ell}$
BC_1 x Loc	$(b_1-1)(\ell-1)$	$\sigma^2_e + r\sigma^2_{g/b_2/b_1\ell} +$
BC_2/BC_1 x Loc	$b_1(b_2-1)(\ell-1)$	$\sigma^2_e + r\sigma^2_{g/b_2/b_1\ell} +$
$Gen/BC_2/BC_1$ x Loc	$b_1b_2(g-1)(\ell-1)$	$\sigma^2_e + r\sigma^2_{g/b_2/b_1\ell}$
Residual	$\ell(r-1)(G-1)$	σ^2_e

[a]Where Loc = locations, Rep = replications, Gen = genotypes, and BC_1 and BC_2 = backcross family one and two, respectively.

[b]Where ℓ = number of locations, r = number of replications, G = number of lines in the population, b_1 = number of BC_1 families, b_2 = number of BC_2 families, and $\bar{g}$ = number of lines in a BC_2 family.

Expected mean squares

$$rg\sigma^2_{b_2/b_1\ell} + rgb_2\sigma^2_{b_1\ell} + r\ell\sigma^2_{g/b_2/b_1} + r\ell g\sigma^2_{b_2/b_1} + r\ell gb_2\sigma^2_{b_1}$$

$$rg\sigma^2_{b_2/b_1\ell} + r\ell\sigma^2_{g/b_2/b_1} + r\ell g\sigma^2_{b_2/b_1}$$

$$r\ell\sigma^2_{g/b_2/b_1}$$

$$rg\sigma^2_{b_2/b_1\ell} + rgb_2\sigma^2_{b_1\ell}$$

$$rg\sigma^2_{b_2/b_1\ell}$$

with partitioning of the variance due to genotypes into sources due to backcross families. Standard errors of the variance component estimates were calculated using the generalized formula (Kempthorne, 1969):

$$\frac{2}{r^2}\left(\frac{(MS_1)^2}{df + 2} + \frac{(MS_2)^2}{df + 2}\right)^{\frac{1}{2}}$$

Comparisons among population means were tested by appropriate F tests and a line in a population was considered a transgressive segregate if it was significantly greater than the high parent or less than the low parent at the 5% level of probability. Expected population means were calculated as a weighted mean of the parent lines in a population, e.g.,

1/8 A. sterilis parent + 1/8 Otter + 1/4 Grundy +

1/2 Noble for the W populations.

Skewness and kurtosis estimates were calculated using the options in the SAS means procedure (SAS, 1979). Phenotypic correlations (r_{ph}) were calculated using line means for pairs of traits and genotypic correlations were calculated using the following formula (Falconer, 1960):

$$r_g = \frac{\hat{\sigma}_{xy}}{(\hat{\sigma}^2_x \cdot \hat{\sigma}^2_y)^{\frac{1}{2}}}$$

where:

$\hat{\sigma}_{xy}$ estimated the genetic covariance for traits x and Y

$\hat{\sigma}^2_x$ and $\hat{\sigma}^2_y$ estimated the genetic variances for traits x and y, respectively.

RESULTS

The 1980 season was ideal for oat production at the AFRC and Hinds Farm, Ames, where overall mean GYD's were 51 and 47 q/ha, respectively (Table 4). GR and HI were 7 and 1% less, respectively, at the Hinds Farm, but plants grew 19% taller under irrigation. Growth conditions at Kanawha were favorable, but the later planting date and a slower growth rate early in the season resulted in an overall mean GYD of only 36 q/ha.

Parental Performance

HD's of the A. sterilis parents ranged from 7.4 to 11.4 days later and HT's 0.4 to 20.2 cm taller than the latest and tallest A. sativa parent, respectively (Table 5). Differences within the species were small except for HD of Wright, which was late among the A. sativa parents, and HT of Wright and PI 318016, which were the tallest and shortest in their respective species groups. GYD's of the A. sativa parents ranged from 3.4 to 8.4 q/ha greater than the highest yielding A. sterilis parents and SYD's, except for PI 317989, were generally much lower for the A. sterilis than for the A. sativa parents. HI values ranged from 39.5 to 48.7% within the A. sativa parental group and 40.9 to 46.7% within the A. sterilis group, so on the average, the two species were not much different for this trait. The A. sativa parents had GR's

Table 4. Mean GYD, SYD, and HI at the three locations and mean GR, HD, and HT at AFRC and Hinds Farm only

Trait	Unit	Location		
		AFRC	Hinds Farm	Kanawha
GYD	q/ha	50.6	46.8	36.1
SYD	q/ha	58.4	56.0	41.1
HI	%	46.4	45.5	46.8
GR[a]	q/da/ha	0.85	0.79	-
HD[a]	days	63.4	62.6	-
HT[a]	cm	91.2	108.2	-

[a]Means based on two replicates at AFRC and one at Hinds Farm.

between 0.95 and 1.35 q/da/ha where the A. sterilis parents ranged from 0.48 to 0.86 q/da/ha.

Grain Yield

Overall, the mean GYD advantage of 3.3 q/ha for C over W populations was significant (Table 6), and it varied between 2.9 q/ha at the AFRC and Hinds Farm, Ames, to 4.1 q/ha at Kanawha. The mean of C1 was significantly larger than the mean of the W populations by 2.3 q/ha, and C2 significantly outyielded C1. C population means were 3 to 14% larger than W population means and W2 had the largest mean GYD within the W group. Cytoplasmic differences were not associated with

Table 5. Means for HD, HT, GYD, SYD, HI, and GR for the six *A. sativa* and four *A. sterilis* parents

Parent	HD	HT	GYD	SYD	HI	GR
	days	cm	q/ha	q/ha	%	q/da/ha
Otter	61.7	90.4	46.2	56.4	45.0	0.97
Grundy	60.5	90.7	49.7	53.1	48.3	0.96
Noble	62.3	91.0	51.2	56.4	47.6	1.02
Lang	60.6	93.0	50.7	53.8	48.7	0.95
Wright	65.6	110.4	50.9	77.9	39.5	1.35
Chief	63.2	101.6	50.6	62.0	44.9	1.09
PI 317789	76.0	125.3	33.7	38.5	46.7	0.48
PI 317973	73.0	130.6	31.5	38.1	45.3	0.53
PI 317989	73.7	126.7	42.8	56.5	43.1	0.86
PI 318016	73.0	110.8	27.1	39.2	40.9	0.55
$L.S.D._{0.05}$	3.3	5.1	9.2	11.2	3.9	0.11

significant GYD differences.

The deviations of the observed from expected population means were all highly significant and negative, and the deviations from expected tended to be larger for the W than for the C populations. Minimum GYD values were similar in all populations except C2, but the numbers of lines with

Table 6. Observed population means, deviations of observed from expected means, and minimum and maximum values for GYD within the six populations

Population	Observed mean	Deviation[a]	Minimum	Maximum
	q/ha			
W1	43.3	-4.8**	12.9	70.2
W2	44.4	-3.3**	10.8	71.8
W3	44.1	-5.1**	16.5	64.2
W4	42.0	-5.3**	11.5	64.4
C1	45.7	-3.3**	14.5	68.0
C2	47.7	-2.2**	22.4	67.6
$L.S.D._{0.05}$	1.2	-	9.7	9.7

[a]Deviation = observed - expected mean.

**Significant at the 1% level.

GYD's less than 21.5 q/ha[1], W1(6)[2], W2(1), W3(1), W4(9), and C1(1) indicated that the low values for W2, W3, and C1 were definitely "outliers". The maximum GYD's in W1 and W2 were larger, and in W3 and W4 were smaller, than the comparable values in C1 and C2, but the numbers of lines with GYD's

[1]Value approximates the highest yielding low line, e.g., 21.5 q/ha, or lowest yielding high line, e.g., 63.5 q/ha, in the six populations.

[2]Figures in parentheses after population designation refer to number of lines in a certain category.

greater than 63.5 q/ha (see footnote 1 on page 27), W1(2), W2(4), W3(1), W4(1), C1(6), C2(9) demonstrated the general superiority of the C populations. Frequency distributions also corroborate the generally higher mean frequencies of lines in the highest GYD class (2.3 versus 0.8%) and lower frequencies of lines in the lowest GYD class (0.3 versus 1.1%) for C and W populations, respectively (Table 7).

Genetic variances for GYD were similar in W1, W2, W3, and C1 (Table 8). The genetic variance of W4 was 16% larger than C1, but W4 was distributed with a highly significant negative skewness (Table 7). The 19% lower genetic variance in C2 relative to C1 resulted from small genetic variances in 3-way crosses where Otter x Noble was the single cross. This will be discussed in greater detail later. Genotype x location variances were significant in all populations and differences in relative magnitudes were not associated with population groups. Nevertheless, the magnitude of the genotype x location variances was small when compared to the genetic variances, and they were not major contributors to GYD variation in any population tested in my experiment.

The percentages of low transgressive segregates and lines yielding less than the low parent varied greatly among the oat populations (Table 9). A. sterilis parents and Otter were the low parents in the W and C populations, respectively. W4 had the greatest frequency of lines with low GYD's;

Table 7. Frequency distributions and associated skewness and kurtosis values for GYD in the six populations

Class midpoint	Population					
	W1	W2	W3	W4	C1	C2
q/ha	----------	----------	----------	%----------	----------	----------
16.7	1.2	0.4	0.4	2.3	0.4	0.2
29.6	13.3	12.5	13.7	16.6	8.4	4.7
42.5	63.7	62.1	59.2	63.1	58.4	52.8
55.4	20.5	24.0	26.4	17.8	30.6	39.9
68.4	1.4	1.00	0.4	0.2	2.2	2.4
Skewness	-0.10	0.04	-0.15	-0.47**	-0.13	-0.11
Kurtosis	1.06	0.66	0.07	1.23	0.66	0.52

**Significant at the 1% level.

Table 8. Genetic variance, genotype x location variance, and associated standard errors for GYD in the six populations

Population	Genetic variance	Genotype x location variance
W1	47.21 ± 3.74	4.89 ± 1.97
W2	43.24 ± 3.62	8.37 ± 2.19
W3	42.53 ± 3.50	7.38 ± 2.03
W4	52.59 ± 4.01	4.28 ± 1.82
C1	45.21 ± 3.65	9.00 ± 1.96
C2	36.80 ± 2.91	4.07 ± 1.83

Table 9. Percentages of lines with GYD's less than the low parent, exceeding the high parent, and exhibiting low and high transgressive segregation in the six populations

Population	Low transgressive segregates[a]	Less than low parent	Exceeding high parent	High transgressive segregates[b]
	----------	%	----------	
W1	1.4	8.2	14.5	1.8
W2	0.2	3.5	17.4	1.4
W3	7.0	43.6	16.8	1.0
W4	1.2	4.5	10.7	0.8
C1	11.6	53.1	22.9	2.8
C2	5.9	40.8	29.0	3.8

[a]Significantly less than low parent at 5% level.

[b]Significantly greater than high parent at 5% level.

nevertheless, few lines were classified as transgressive segregates, which reflects the very low yield of the low parent value. W2 and W3 had comparable population means and frequencies of low-yielding lines (Table 7), but the difference in their respective low parent values was reflected in percentages of low transgressive segregates. Thus, for W2, W3, and to a degree, W1, the small percentages of low transgressive segregates were a function of the GYD of the low parent superimposed on similar distributions. Although the percentages of lines in C1 and C2 that yielded less than

Otter were 53 and 41%, respectively, there was a twofold difference in the percentage of low transgressive segregates in the two populations. There were distinct differences in percentages of high transgressive segregates and of lines exceeding the high parent (Noble in all populations) in the W and C groups. W1, W2, and W3 had 15 to 17% of their lines exceed Noble, while W4 had only 11%. C1 and C2 had 23 and 29%, respectively. Similarly, C1 and C2 had 2.8 and 3.8% high transgressive segregates while the W populations had only from 0.8% (W4) to 1.8% (W1).

Phenotypic and genotypic correlations of GYD with the other agronomic traits are shown in Table 10. Note that, in most cases, the phenotypic and genotypic correlations for a pair of traits within a population are similar, indicating that correlations due to nonadditive effects were small. Correlations between GYD and SYD ranged between 0.7 and 0.8 for both phenotypic and genotypic correlations. W4 displayed a stronger association between GR and GYD than did the other populations, primarily due to the presence of a greater frequency of low GR-low GYD lines. Generally, there was a stronger association between HI and GYD in the W than in the C populations. W1 and W4 had more low GYD-low HI lines, and all W populations tended to have fewer lines with mediocre GYD and both high and low HI values. In other words, a strong association between GYD and HI is a characteristic of

Table 10. Phenotypic (upper) and genotypic (lower) correlations of SYD, GR, HI, HT, and HD with GYD in the six populations

Population	SYD	GR	HI	HT	HD
W1	0.75**	0.65	0.31	0.46	0.40
	0.75	0.73	0.33	0.56	0.48
W2	0.72	0.61	0.37	0.42	0.40
	0.71	0.69	0.41	0.52	0.44
W3	0.68	0.65	0.39	0.32	0.18
	0.66	0.70	0.44	0.39	0.19
W4	0.82	0.77	0.33	0.46	0.36
	0.82	0.86	0.34	0.54	0.40
C1	0.73	0.65	0.19	0.54	0.47
	0.73	0.73	0.18	0.64	0.55
C2	0.70	0.60	0.15	0.40	0.38
	0.69	0.67	0.13	0.46	0.45

**All phenotypic correlations significant at 1% level.

populations with sizable proportions of unadapted germplasm. Characteristically, GYD is positively correlated with HT and HD as demonstrated by C1 and C2, but the W populations tended to have more tall HT-low GYD lines than did C1. The association between GYD and HD was similar for W1, W2, C1, and C2, but the W populations in general, and W3 in particular, had higher frequencies of low- to mediocre-yielding late-maturing lines than did the C populations. C2 had a greater frequency of lines with high GYD's and HD's less than 65 days than did C1.

Straw Yield

The overall mean SYD advantage of 4.6 q/ha for C over W populations was significant (Table 11); the advantage varied from 6.1 q/ha at the AFRC, to 5.2 q/ha at the Hinds Farm, to 2.5 q/ha at Kanawha. The mean of C1 was larger than the mean of the W populations by 2.8 q/ha and the mean of W1 and W2, with A. sativa cytoplasm, significantly outyielded the mean of W3 and W4, with A. sterilis cytoplasm, by 2.3 q/ha. C population means were 2 to 19% larger than W population means and W2 had the largest SYD within the W group. C2 significantly outyielded C1.

The deviations of observed from expected population means were all significantly negative, with the exception of W2. Deviations in W3 and W4 were larger than in W1 and W2, which were of similar magnitude to deviations in the C populations.

Lines with minimum SYD's in W1 and W4 were lower by a sizable amount than in the other populations, but the numbers of lines with SYD's less than 32.5 q/ha, W1(6), W2(2), W3(1), W4(17), C1(6), and C2(1), showed that W4 was exceptional in its frequency of low-yielding lines. The mean of maximum values in the C populations was 14 q/ha greater than the mean in the W populations, and the numbers of lines with SYD's greater than 77 q/ha, W1(2), W2(4), W3(3), W4(5), C1(17), C2(23), demonstrated the superiority of the C

Table 11. Observed population means, deviations of observed from expected means, and minimum and maximum values for SYD within the six populations

Population	Observed mean	Deviation[a]	Minimum	Maximum
	q/ha			
W1	50.7	-2.6*	14.9	82.2
W2	52.2	-1.1	29.3	77.9
W3	50.9	-4.7**	30.9	78.2
W4	47.5	-6.0**	19.2	82.9
C1	53.1	-2.2*	27.3	94.2
C2	56.7	-3.2**	32.3	93.8
$L.S.D._{0.05}$	2.1	-	13.0	13.0

[a]Deviation = observed - expected mean.

**Significant at the 1% level.

*Significant at the 5% level.

populations for vegetative vigor. W1 and W4, with a mean of 0.5%, were the only W populations with lines in the highest SYD class, whereas the mean was 3.0% for the C populations (Table 12). C2 and W3 had no lines in the lowest SYD class, but W1, W2, and W4 had a mean of 1.4% compared to 0.4% for C1. All populations had an excess of values greater than the mean, indicated by their significant positive skewness. In addition, W4 and C1 had significant positive kurtosis, which

Table 12. Frequency distributions and associated skewness and kurtosis values for SYD in the six populations

Class midpoint	Population					
	W1	W2	W3	W4	C1	C2
q/ha	----------	----------	----------	%----------	----------	----------
22.6	1.2	0.4	0.0	2.5	0.4	0.0
38.8	36.5	29.9	35.7	49.4	29.8	19.3
54.9	49.8	56.1	53.3	39.8	54.1	52.8
71.0	12.3	13.7	10.9	7.4	12.7	24.8
87.2	0.2	0.0	0.0	0.8	2.9	3.1
Skewness	0.38**	0.37**	0.48**	0.65**	0.68**	0.43**
Kurtosis	0.18	-0.15	-0.03	0.79**	0.82**	-0.05

**Significant at the 1% level.

indicated an excess of values near the mean, far from the mean, and a corresponding depletion of the flanks of the distribution curve.

The mean genetic variance for SYD in the C populations was 32% greater than the mean of the W populations (Table 13). W1 and W4 had the largest genetic variances among the W populations. The genetic variance of C1 was 5% greater than C2. W4 was the only population with a nonsignificant genotype x location variance, but as with GYD, the magnitudes of the interaction variances were small when compared to the genetic variances.

Table 13. Genetic variance, genotype x location variance and associated standard errors for SYD in the six populations

Population	Genetic variance	Genotype x location variance
W1	76.04 ± 6.16	7.66 ± 3.52
W2	61.22 ± 5.41	15.20 ± 3.75
W3	62.11 ± 5.33	12.13 ± 3.50
W4	82.36 ± 6.15	-
C1	95.15 ± 7.45	13.93 ± 3.63
C2	90.72 ± 6.92	9.70 ± 3.90

The low parents in W1, W2, and W4 were the respective A. sterilis parents, all of which had similar SYD's (Table 5), and W4, with a small mean and large variance, had the highest percentage of low transgressive segregates among these three populations (Table 14). W2, with the largest W population mean and small variance, had no low transgressive segregates and only 5.0% of its lines yielded less than the low parent. The low parent for SYD in W3, C1, and C2 was Grundy. W3 had 9% more of its lines yield less than Grundy, and 3% more low transgressive segregates, then did C1. C2, with two high SYD parents, had 4.5% low transgressive segregates and 40.3% of its lines yielded less than Grundy.

Otter and Noble had the same SYD's (Table 5), and were

Table 14. Percentages of lines with SYD's less than the low parent, exceeding the high parent, and exhibiting low and high transgressive segregation in the six populations

Population	Low transgressive segregates[a]	Less than low parent	Exceeding high parent	High transgressive segregates[b]
	----------%----------			
W1	0.6	8.4	27.7	5.9
W2	0.0	5.1	31.3	4.7
W3	15.0	62.9	24.6	3.9
W4	1.2	18.4	16.4	4.7
C1	11.6	53.5	35.5	8.0
C2	4.5	40.3	3.7	0.2

[a]Significantly less than low parent at 5% level.

[b]Significantly greater than high parent at 5% level.

the high parents in all populations except C2. There was a twofold difference among the W populations in the percentages of lines that exceeded the high parents, but all of them had between 4% and 6% high transgressive segregates. C1, with 36% of its lines exceeding the high parent and 8% transgressive segregates, was superior to all W populations in respect to both of these criteria. Wright, with a SYD of 78 q/ha, was the high parent in C2 and only one line in that population significantly exceeded it. Nevertheless, 14% of the lines in C2 significantly exceeded the SYD of Otter and Noble,

the high parents in the other five populations.

Phenotypic and genotypic correlations between SYD and GR were high in all populations, but the genotypic was always higher than the comparable phenotypic (Table 15). C populations had stronger negative associations between SYD and HI than did the W populations. C1 had a higher frequency of high SYD-low HI lines than W2 or W4, and W4 also had a high frequency of low SYD-low HI lines. The phenotypic and the genotypic correlations between SYD and HT were similar for all populations with phenotypic correlations ranging from 0.6 to 0.7 and genotypic correlations from 0.7 to 0.8. Similarly, SYD and HD correlations were comparable in all populations with phenotypic correlations ranging from 0.5 to 0.7 and genotypic correlations from 0.6 to 0.8.

Growth Rate

The mean GR advantage of 0.08 q/da/ha for C over W populations was highly significant (Table 16). C1 and C2 had GR means that were 0.05 and 0.11 q/da/ha, respectively, greater than the mean of the W populations. W2, which had the highest mean GR among the W populations with a mean of 0.92 q/da/ha, was equal to C1 for this trait. The mean of C2, which had Wright as the high GR parent (Table 5), was significantly greater than the mean of C1.

Deviations of observed from expected means were

Table 15. Phenotypic (upper) and genotypic (lower) correlations of GR, HI, HT, and HD with SYD in the six populations

Population	GR	HI	HT	HD
W1	0.87**	-0.38	0.68	0.55
	0.97	-0.37	0.75	0.64
W2	0.86	-0.36	0.59	0.59
	0.95	-0.34	0.69	0.71
W3	0.87	-0.39	0.62	0.53
	0.97	-0.39	0.74	0.62
W4	0.89	-0.25	0.66	0.59
	0.97	-0.23	0.75	0.66
C1	0.91	-0.51	0.73	0.65
	0.98	-0.52	0.84	0.73
C2	0.90	-0.59	0.69	0.65
	0.98	-0.62	0.77	0.77

**All phenotypic correlations significant at 1% level.

significant and negative for all populations except W2. W1, C1, and C2, which had deviations of similar magnitude, i.e., 0.06-0.07 q/da/ha, were notably smaller than the deviations of W3 and W4. The minimum GR line in W1 was a single "outlier", but the number of lines in each population with GR less than 0.58 q/da/ha, W1(12), W2(4), W3(8), W4(26), C1(7), C2(0), and the characteristics of the frequency distributions (Table 17) indicated that W1, W3, and W4 had the highest frequencies of low GR lines. W3 had two very high GR lines, but the C populations had the highest GR lines in the

Table 16. Observed population means, deviations of observed from expected means, and minimum and maximum values for GR within the six populations

Population	Observed mean	Deviation[a]	Minimum	Maximum
	q/da/ha			
W1	0.87	-0.06**	0.26	1.38
W2	0.92	-0.02	0.53	1.44
W3	0.88	-0.10**	0.47	1.50
W4	0.82	-0.12**	0.39	1.43
C1	0.92	-0.06**	0.45	1.69
C2	0.98	-0.07**	0.58	1.60
$L.S.D._{0.05}$	0.01	-	0.27	0.27

[a]Deviation = observed - expected mean.

**Significant at the 1% level.

study, at 1.69 and 1.60 q/da/ha. The number of lines with GR's greater than 1.38 q/da/ha, W1(0), W2(2), W3(2), W4(1), C1(8), C2(7), and the distribution of high GR lines (Table 17) demonstrated the superiority of the C populations for this trait. As with SYD, all populations had significant positive skewness, or an excess of values above the mean, while W4, C1, and W1 had significant positive kurtosis, or an excess of values close to the mean.

The genetic variances of W1, W4, and C2 were similar in

Table 17. Frequency distributions and associated skewness and kurtosis values for GR in the six populations

Class midpoint	Population					
	W1	W2	W3	W4	C1	C2
q/da/ha	----------	----------	----------	% ----------	----------	----------
0.32	0.8	0.0	0.2	1.2	0.4	0.0
0.65	35.0	23.8	35.0	50.0	27.1	16.8
0.97	55.9	67.0	57.2	44.9	59.8	62.3
1.29	8.4	9.2	7.4	3.9	11.8	20.3
1.62	0.0	0.0	0.2	0.0	1.0	0.5
Skewness	0.38**	0.32**	0.46**	0.58**	0.65**	0.34**
Kurtosis	0.46*	0.14	0.29	0.89**	0.90**	-0.29

**Significant at the 1% level.

*Significant at the 5% level.

magnitude; W2 and W3 had the smallest variances; and C1 the largest (Table 18). The variance of C2 was 17% less than the variance of C1, and the overall mean genetic variance of W populations was 24% less than the mean variance of C populations.

The A. sterilis lines were the low parents in each W population for GR. W1, W2, and W4 had low parent values of only 0.50 to 0.55 q/da/ha, and few or no low transgressive segregates were found in these populations, whereas W3 had a low parent value of 0.86 q/ha/da and 7.4% low transgressive

Table 18. Genetic variances and associated standard errors for GR in the six populations

Population	Genetic variance
W1	0.019 ± 0.002
W2	0.014 ± 0.001
W3	0.016 ± 0.001
W4	0.018 ± 0.001
C1	0.024 ± 0.002
C2	0.020 ± 0.002

Table 19. Percentages of lines with GR's less than the low parent, exceeding the high parent, and exhibiting low and high transgressive segregation in the six populations

Population	Low transgressive segregates[a]	Less than low parent	Exceeding high parent	High transgressive segregates[b]
	----------%----------			
W1	0.2	0.8	18.2	3.7
W2	0.0	0.0	24.0	3.1
W3	7.4	49.8	18.8	2.5
W4	0.0	3.5	11.1	2.3
C1	17.5	62.8	28.2	6.3
C2	6.4	46.7	2.1	0.2

[a]Significantly less than low parent at 5% level.

[b]Significantly greater than high parent at 5% level.

segregates (Table 19). Differences among the A. sativa parents for GR were small, with the exception of Wright, and the low parent values in C1 and C2 were 0.96 and 0.95 q/da/ha for Grundy and Lang, respectively. The difference between the distributions of low GR lines in C1 and C2 may have resulted from the influence of the parent, Wright, a high GR cultivar, on C2. Noble was the high parent in the W populations and in C1. W1 and W2 had 3.7 and 3.1% high transgressive segregates, but C1 had the highest frequency of lines that exceeded Noble and 6.3% high transgressive segregates. The W populations with A. sativa cytoplasm had, overall, 1% more high transgressive segregates than W populations with A. sterilis cytoplasm. Only one line in C2 had a significantly larger GR than Wright, but 38% exceeded Noble and 9% were significantly greater than Noble, the high parent in all other populations.

In all populations, there were negative phenotypic and genotypic correlations between GR and HI, but the associations were of lesser magnitude in the W than in the C populations (Table 20). C populations tended to contain more high GR-low HI lines and fewer low GR-low HI lines than did W populations, particularly W3 and W4. Phenotypic and genotypic correlations between GR and HT were similar in all populations, ranging from 0.5-0.6 and 0.6-0.8, respectively. C populations tended to have more high GR-late HD lines than did W populations and

Table 20. Phenotypic (upper) and genotypic (lower) correlations of HI, HT, and HD with GR in the six populations

Population	HI	HT	HD
W1	-0.34**	0.57	0.31
	-0.47	0.68	0.42
W2	-0.33	0.49	0.31
	-0.42	0.63	0.45
W3	-0.27	0.53	0.27
	-0.39	0.65	0.39
W4	-0.15	0.56	0.34
	-0.21	0.66	0.44
C1	-0.48	0.64	0.46
	-0.64	0.76	0.57
C2	-0.55	0.56	0.46
	-0.69	0.68	0.62

**All phenotypic correlations significant at 1% level.

W3 had a high frequency of late HD-low GR lines. This resulted in a stronger association between GR and HD in C than in W populations.

Harvest Index

There were no significant differences among the means for HI for the six populations, for W vs C populations, or for cytoplasms. For example, the population means ranged between 46 and 47% (Table 21). The W populations had lower GYD's and SYD's than C populations, but the overall relationship between

Table 21. Observed population means, deviations of observed from expected means, and minimum and maximum values for HI within the six populations

Population	Observed mean	Deviation[a]	Minimum	Maximum
		-----------%-----------		
W1	46.2	-1.3*	30.6	54.9
W2	46.0	-1.2*	19.8	52.5
W3	46.5	-0.6	31.2	54.6
W4	47.0	0.3	29.9	53.8
C1	46.6	-0.5	29.2	54.1
C2	46.2	0.3	35.8	55.8
$L.S.D._{0.05}$	-		4.2	4.2

[a]Deviation = observed - expected mean.

*Significant at 5% level.

grain and straw remained constant over all populations. There was a significant interaction of population type (i.e., W vs C) with locations. W populations had overall HI means 0.89 and 0.61% greater than the C populations at the AFRC and Hinds Farm, Ames, respectively, but 1.4% less at Kanawha. Thus, as the production environment became more stressed, the C populations produced relatively more GYD by translocating a larger portion of their photosynthate into grain than did the W populations.

Four populations, W1, W2, W3, and C1, had mean HI's that deviated negatively from expected values, but only W1 and W2 deviated significantly. The minimum HI value in W2, at 19.8%, was a single "outlier" and the number of lines with a HI less than 36%, W1(6), W2(3), W3(5), W4(5), C1(7), and C2(1), showed that all populations had similar characteristics for low values in the frequency distributions. Maximum values for HI were similar in W (i.e., 53-55%) and C (i.e., 54-56%) populations, respectively, but the numbers of lines with a HI greater than 52%, W1(10), W2(7), W3(18), W4(17), C1(16), C2(18), and the frequency distributions (Table 22) illustrated a distinct inferiority for this trait in W1 and W2 vs the other populations. All populations had significant negative skewness, and excepting C2, all had significant positive kurtosis because HI values tended to be distributed close to the population means. The range of HI values was approximately 30-50% with a mean of 46%. Incidentally, 46% is considered to be the optimum for oats grown in Iowa.

Mean genetic variances of W and C populations were 9.43 and 9.36, respectively (Table 23). In general, the magnitude of genetic variances among the six oat populations was quite similar for HI. The genetic variances were five to eight times larger than the genotype x location variances.

Table 22. Frequency distributions and associated skewness and kurtosis values for HI in the six populations

Class midpoint	Population					
	W1	W2	W3	W4	C1	C2
%	----------	----------	----------	----------	----------	----------
23	0.0	0.2	0.0	0.0	0.0	0.0
31	1.0	0.4	0.6	0.6	1.0	0.0
39	14.1	14.1	13.9	9.2	11.4	16.5
47	79.7	81.5	77.2	81.5	80.8	76.2
55	5.3	3.9	8.4	8.8	6.9	7.3
Skewness	-0.91**	-1.61**	-0.80**	-1.10**	-1.03**	-0.30**
Kurtosis	2.11**	8.31**	1.44**	2.63**	2.66**	-0.01

**Significant at the 1% level.

Table 23. Genetic variances, genotype x location variances, and associated standard errors for HI in the six populations

Population	Genetic variance	Genotype x location variance
W1	9.61 ± 0.75	1.77 ± 0.35
W2	9.12 ± 0.72	1.39 ± 0.36
W3	10.45 ± 0.80	1.87 ± 0.35
W4	8.55 ± 0.68	1.33 ± 0.35
C1	9.55 ± 0.75	1.90 ± 0.40
C2	9.18 ± 0.67	1.23 ± 0.32

The low HI parent in W1, W2, and C1 was Otter, and the three populations had similar percentages of low transgressive segregates (Table 24). W1 and W2, however, had a greater percentage of lines with HI's less than the low parent than did C1. The percentages of low transgressive segregates reflected the low parent values in the other populations, W3 (43.1%), W4 (40.9%), and C2 (39.5%). However, the percentages of lines less than Grundy were similar in all six populations. The high parent in C2 was Lang (48.7%) and in the other populations it was Grundy (48.3%). Overall, W1 and W2 had 8.0% fewer lines exceeding Grundy than W3 and W4. Percentages of high transgressive segregates varied from 0.2% for W2 to 2.8% for C1, and W1, W3, W4, and C2 had approximately 2.0%.

There were differences in the correlations between HI and HT among the six populations (Table 25). W2 had low values relative to the other W populations and C2 had high values relative to all other populations. Genotypic correlations were between -0.3 to -0.5 for W populations and -0.6 for C populations. Phenotypic correlations between HI and HD ranged from -0.2 to -0.5. Genotypic correlations were between -0.3 to -0.5 for W populations and -0.5 to -0.6 for C populations.

Table 24. Percentages of lines with HI's less than the low parent, exceeding the high parent, and exhibiting low and high transgressive segregation in the six populations

Population	Low transgressive segregates[a]	Less than low parent	Exceeding high parent	High transgressive segregates[b]
	----------%----------			
W1	6.6	32.2	24.4	1.8
W2	6.3	33.0	23.1	0.2
W3	3.9	14.7	28.5	2.3
W4	1.2	5.3	35.4	1.6
C1	5.7	25.5	30.4	2.8
C2	0.0	3.0	23.6	1.9

[a]Significantly less than low parent at 5% level.

[b]Significantly greater than high parent at 5% level.

Plant Height

The mean HT of the W populations was significantly larger than the mean of the C populations (Table 26). The A. sterilis parents of W1, W2, and W3 had similar HT's at 125-131 cm, whereas the A. sterilis parent of W4 was only 111 cm (Table 5). Note that W4 had the lowest population mean for HT among the W populations. The mean of C2 was significantly greater than C1, and two of its parents, Wright and Chief, are tall A. sativa cultivars (Table 5).

All deviations of observed means from expected values

Table 25. Phenotypic (upper) and genotypic (lower) correlations of HT and HD with HI in the six populations

Population	HT	HD
W1	-0.35**	-0.25
	-0.39	-0.33
W2	-0.23	-0.22
	-0.29	-0.37
W3	-0.38	-0.42
	-0.48	-0.54
W4	-0.32	-0.36
	-0.40	-0.48
C1	-0.39	-0.35
	-0.55	-0.48
C2	-0.52	-0.48
	-0.62	-0.62

**All phenotypic correlations significant at 1% level.

were positive and significant. W2 and C1 had the largest deviations and W1, W3, and C2 had similar deviations, so the magnitude of the deviation was unrelated to specific parental combination of *sativa* vs *sterilis* germplasm.

Minimum HT values in W1, W4, and C1 were single "outliers"; nevertheless, these three populations did have the highest frequencies of short lines (Table 27). W populations had greater ranges for HT than did C populations. W1, W2, and C2 had the highest frequencies of tall lines (Table 27). All populations had significant positive skewness; and W1 and W3 had significant positive kurtosis. C2 had significant

Table 26. Observed population means, deviations of observed from expected means and minimum and maximum values for HT within the six populations

Population	Observed mean	Deviation[a]	Minimum	Maximum
		%		
W1	97.2	2.0**	72.0	136.0
W2	99.8	4.0**	75.3	129.3
W3	97.3	2.1**	74.7	134.3
W4	94.5	1.2**	66.7	125.3
C1	94.4	3.7**	70.7	117.3
C2	98.0	1.9**	76.7	128.0
$L.S.D._{0.05}$	1.0		9.0	9.0

[a]Deviation = observed - expected mean.

**Significant at the 1% level.

negative kurtosis, which indicated that its distribution curve had a flatter top than the normal.

There was nearly a twofold range in genetic variances among populations, and overall, W populations had a mean genetic variance 36% greater than C1 but 16% less than C2 (Table 28). The larger variances in W1, W2, W3, and also C2 were due to greater frequencies of lines at the upper end of the frequency distributions (Table 27).

W4 and C1, with similar population means, had the largest

Table 27. Frequency distributions and associated skewness and kurtosis values for HT in the six populations

Class midpoint	Population					
	W1	W2	W3	W4	C1	C2
cm	----------	----------	----------	%----------	----------	----------
73	2.9	0.6	1.0	3.9	2.9	1.2
88	45.5	35.8	43.4	56.6	59.4	45.7
103	42.0	48.2	48.6	34.4	33.9	40.3
118	8.4	14.5	6.6	5.1	3.7	12.2
133	1.2	1.0	0.4	0.0	0.0	0.7
Skewness	0.60**	0.50*	0.46**	0.47**	0.35**	0.46**
Kurtosis	0.58**	0.00	0.78**	0.32	-0.13	-0.36*

**Significant at the 1% level.

*Significant at the 5% level.

Table 28. Genetic variances and associated standard errors for HT in the six populations

Population	Genetic variance
W1	91.55 ± 6.50
W2	78.94 ± 5.64
W3	62.27 ± 4.57
W4	73.52 ± 5.29
C1	56.21 ± 4.11
C2	91.17 ± 5.96

percentages of lines less than the low parent (Otter in all populations) and low transgressive segregates (Table 29). W1, W3, and C2 had similar population means and their percentages of low transgressive segregates ranged from 3.5 to 6.3%. W2, with the largest population mean, had the fewest transgressive segregates. The A. sterilis lines were the high parents in each W population, and Noble and Wright were the high parents in C1 and C2, respectively. W1, W2, and W3 had few or no lines significantly taller than the A. sterilis parents. Although W4 and C2 had similar high parent values, C2 had more lines exceed the high parent and exhibit high transgressive segregation than W4. Only 0.6 cm separated the low and high parent in C1; nevertheless, a large amount of variability for HT was expressed in this population. The percentages of lines in each population significantly exceeding Wright, the tallest A. sativa parent, were W1 (3.5%), W2 (4.3%), W3 (1.0%), W4 (1.6%), C1 (0.2%), and C2 (3.5%).

Phenotypic correlations between HT and HD were between 0.6-0.7 in W populations and were 0.8 in C populations (Table 30). C populations tended to have fewer tall lines with early to medium HD than W populations. Genotypic correlations were from 0.6 to 0.7 for W populations and 0.8 for C populations.

Table 29. Percentages of lines with HT's less than the low parent, exceeding the high parent, and exhibiting low and high transgressive segregation in the six populations

Population	Low transgressive segregates[a]	Less than low parent	Exceeding High parent	High transgressive segregates[b]
	----------%----------			
W1	6.3	24.4	1.2	0.2
W2	2.3	14.8	0.0	0.0
W3	3.5	19.3	0.4	0.2
W4	8.2	36.3	4.5	1.2
C1	8.2	33.7	62.6	30.4
C2	5.2	26.2	12.9	3.5

[a]Significantly less than low parent at 5% level.

[b]Significantly greater than high parent at 5% level.

Heading Date

The W populations and C1 had HD means of 63 days (Table 31). C2 had a mean of 64 days and two of its parents, Chief and Wright, were medium to late in maturity (Table 5). Deviations of observed HD means from expected values were negative for all W populations and significantly positive for the two C populations. The differences among deviations were small, but the difference between the W and C populations was 1.3 days.

Table 30. Phenotypic (upper) and genotypic (lower) correlations of HD with HT in the six populations

Population	HD
W1	0.60**
	0.63
W2	0.55
	0.58
W3	0.60
	0.63
W4	0.65
	0.68
C1	0.75
	0.80
C2	0.77
	0.81

**All phenotypic correlations significant at 1% level.

Minimum HD values in the W populations were 1-2 days earlier than those in the C populations, but the number of lines with HD's less than 58 days, W1(26), W2(26), W3(12), W4(26), C1(2), C2(6), showed W3 deviated from the other W populations, however. W1, W2, and W4 had a higher frequency of early lines than W3, C1, or C2 (Table 32). The numbers of lines with HD's later than 74 days, W1(0), W2(3), W3(1), W4(10), C1(6), C2(3), and the frequency distributions (Table 32) illustrated that W1 and W3 had fewer late HD lines than the other populations. The maximum values in W2 and W3

Table 31. Observed population means, deviations of observed from expected means, and minimum and maximum values for HD within the six populations

Population	Observed mean	Deviation[a]	Minimum	Maximum
	days			
W1	62.7	-0.9**	55.3	73.7
W2	62.8	-0.4	56.0	78.0
W3	63.2	-0.1	55.0	79.3
W4	63.0	-0.1	55.3	79.0
C1	63.3	1.8**	57.0	76.7
C2	64.0	1.6**	56.7	75.0
$L.S.D._{0.05}$	0.2		2.5	2.5

[a]Deviation = observed - expected mean.

**Significant at the 1% level.

were single "outliers".

The genetic variances for HD of W1, C1, and C2 were similar (Table 33). W2 and W4 had variances 18 and 39% greater than C1. All populations had significant positive skewness and W2, W3, W4, and C1 had significant positive kurtosis.

W1, W2, and W4 had similar percentages of lines earlier than Grundy, the earliest parent in all populations (Table 34). C2 had more early transgressive segregates than C1,

Table 32. Frequency distributions and associated skewness and kurtosis values for HD in the six populations

Class midpoint	Population					
	W1	W2	W3	W4	C1	C2
days	----------	----------	----------	%----------	----------	----------
57	17.4	15.6	7.8	17.6	7.7	5.7
62	55.1	57.8	62.7	53.7	64.5	54.2
67	23.8	21.7	25.6	23.1	23.5	34.7
72	3.7	4.5	3.7	3.9	3.1	5.0
77	0.0	0.4	0.2	1.8	1.2	0.4
Skewness	0.57**	0.89**	0.78**	1.07**	1.16**	0.57**
Kurtosis	-0.01	0.82**	1.18**	1.66**	1.81**	0.12

**Significant at the 1% level.

Table 33. Genetic variances and associated standard errors for HD in the six populations

Population	Genetic variance
W1	10.55 ± 0.72
W2	11.98 ± 0.80
W3	9.32 ± 0.64
W4	14.06 ± 0.94
C1	10.13 ± 0.67
C2	10.18 ± 0.64

Table 34. Percentages of lines with HD's less than the low parent, exceeding the high parent, and exhibiting low and high transgressive segregation in the six populations

Population	Low transgressive segregates[a]	Less than low parent	Exceeding high parent	High transgressive segregates[b]
	----------%----------			
W1	4.1	27.5	0.0	0.0
W2	5.1	28.9	1.2	0.2
W3	2.3	17.2	0.2	0.2
W4	3.3	27.3	2.3	1.2
C1	0.4	17.7	51.2	25.9
C2	1.0	13.7	30.2	7.6

[a]Significantly less than low parent at 5% level.

[b]Significantly greater than high parent at 5% level.

but W populations outproduced the C populations in early transgressive segregates. The A. sterilis parents were the high parents in the W populations, which produced few or no high transgressive segregates. Noble and Wright, with HD's of 62.3 and 65.6 days, respectively, were the high parents in C1 and C2. However, the numbers of lines with HD's significantly exceeding Wright, W1(37), W2(45), W3(38), W4(48), C1(43), C2(44), showed little difference among the six populations.

Agronomic Characteristics of Superior Lines for GYD, GR, and SYD

Fifteen lines with the highest GYD's were selected from each population and the means for their agronomic characteristics are given in Table 35. First, the C populations had larger GYD means for the 15 highest GYD lines by 1 to 5 q/ha than did the W populations. Also, the mean of W1 and W2 was 2 q/ha greater than the mean of W3 and W4. Substantial differences in SYD means separated the W and C groups. The lower SYD's in the W populations were associated with smaller GR's, slightly larger HI's, and HD's of 1-3 days earlier. Large differences in HT occurred within and between groups and W1 and W2 were taller than W3 and W4.

Selection of lines on the basis of GR caused a dramatic reduction in the GYD means for populations. Overall, W populations had a GR mean that was ca. 9% less than the mean of the C populations (Table 36). The SYD of W populations averaged 13% less and HI averaged 2% greater than the means of the C populations. Means of HD tended to be earlier for W than for C populations.

Selection for SYD did not result in particularly high GYD means for any population (Table 37). Means for SYD and GR were low in the W populations but HI means were 1-4% larger in W than in C populations. Therefore, assuming that photosynthetic activity remained constant before and after

Table 35. Means of GYD, SYD, GR, HI, HT, and HD for the 15 highest GYD lines in each of the six populations

Population	GYD	SYD	GR	HI	HT	HD
	q/ha	q/ha	q/da/ha	%	cm	days
W1	61.4	70.7	1.14	46.8	111.1	67.7
W2	62.0	66.8	1.14	48.3	107.9	64.6
W3	59.9	67.0	1.12	47.6	104.1	65.1
W4	59.2	68.9	1.13	46.6	104.2	66.8
C1	63.3	74.4	1.20	46.4	105.2	68.2
C2	64.3	76.1	1.26	46.2	109.0	67.6
$L.S.D._{0.05}$	3.1	4.1	0.06	1.3	2.9	0.6

Table 36. Means of GYD, SYD, GR, HI, HT, and HD for the 15 highest GR lines in each of the six populations

Population	GYD	SYD	GR	HI	HT	HD
	q/ha	q/ha	q/da/ha	%	cm	days
W1	53.6	70.5	1.30	43.4	106.8	65.4
W2	54.7	71.5	1.30	43.5	111.2	66.9
W3	52.7	70.9	1.28	42.8	104.9	65.0
W4	53.7	72.4	1.26	43.0	106.8	67.2
C1	55.6	82.7	1.43	40.5	107.0	67.4
C2	55.3	80.6	1.40	41.2	110.0	68.2
$L.S.D._{0.05}$	3.1	4.1	0.06	1.3	2.0	0.6

Table 37. Means of GYD, SYD, GR, HI, HT, and HD for the 15 highest SYD lines in each of the six populations

Population	GYD	SYD	GR	HI	HT	HD
	q/ha	q/ha	q/da/ha	%	cm	days
W1	59.2	74.8	1.23	44.4	110.5	66.9
W2	56.6	75.1	1.25	43.1	113.8	68.6
W3	52.5	74.6	1.22	41.3	108.6	67.0
W4	55.2	74.8	1.23	42.7	108.3	68.4
C1	55.8	84.4	1.41	40.0	108.7	68.5
C2	56.1	84.5	1.35	40.4	111.1	69.0
$L.S.D._{0.05}$	3.1	4.1	0.06	1.3	2.0	0.6

anthesis, the W populations consistently demonstrated more efficient photosynthate partitioning by converting a larger proportion of their photosynthate into grain.

Selection of Agronomically Desirable Lines

Lines were selected from each population with the cultivar Noble used as the standard check. To be selected, a line was required to possess a HD no later, a HT no taller, and a GYD equal to or greater than Noble. Agronomically desirable lines were selected with greater frequency from C than from W populations, but the highest GYD line, 14% greater than Noble, came from W3 (Table 38). Lines with GYD's 10%

Table 38. Numbers of selected lines and their agronomic characteristics in each of the six populations, and the cultivar Noble

Pop.	No. of selected lines	GYD	GYD%[a]	SYD	GR	HI	HT	HD
		q/ha	%	q/ha	q/da/ha	%	cm	days
W1	1	51.1	100	43.1	0.94	54.9	91.3	58.7
W2	3	50.8	99	50.6	0.92	49.9	90.7	59.0
		52.7	103	49.7	0.88	51.6	90.0	62.3
		56.2	110	56.0	1.01	49.9	90.7	62.3
W3	6	50.9	99	51.7	1.07	49.6	90.0	58.7
		51.3	100	52.2	0.86	49.7	89.3	60.7
		51.5	101	52.2	0.96	49.9	86.7	61.0
		55.4	108	54.2	0.86	50.7	88.0	60.7
		56.3	110	52.9	0.81	51.7	80.7	62.0
		58.1	114	48.4	0.80	54.6	91.3	60.3
W4	1	54.2	106	54.0	0.86	50.8	88.7	62.3
C1	12	50.8	99	56.3	1.10	47.7	91.3	61.0
		50.8	99	61.9	1.04	45.1	87.3	60.7
		50.9	99	61.7	1.16	45.1	90.0	61.3
		51.3	100	57.4	0.95	47.0	89.3	59.7
		52.0	102	51.1	0.76	50.6	86.7	61.7
		52.6	103	50.4	0.88	51.9	88.7	61.3
		52.9	103	56.9	1.09	49.0	90.7	62.0
		53.1	104	55.8	1.03	49.1	88.0	60.3
		53.1	104	64.0	1.16	45.9	90.0	61.0
		53.3	104	63.3	1.12	45.5	87.3	61.0
		54.0	106	62.1	1.11	46.8	90.0	59.3
		54.2	106	54.7	0.89	49.9	89.3	61.0
C2	18	50.8	99	45.2	0.85	53.2	90.0	61.3
		51.1	100	51.1	0.93	50.3	90.0	59.0
		51.3	100	46.8	0.81	52.6	86.7	60.7
		51.3	100	52.2	0.95	50.2	86.7	60.0
		51.5	101	66.7	1.19	44.0	86.7	61.0
		51.5	101	46.3	0.87	52.9	90.0	61.3
		51.7	101	58.7	1.16	47.0	85.3	60.0

[a]Expressed as a percentage of Noble.

Table 38. (Continued)

Pop.	No. of selected lines	GYD	GYD%	SYD	GR	HI	HT	HD
		q/ha	%	q/ha	q/da/ha	%	cm	days
		51.9	101	54.0	0.92	49.3	88.7	62.0
		52.9	103	55.6	0.96	48.8	90.7	60.3
		53.1	104	65.5	1.07	45.7	88.3	62.3
		53.3	104	50.9	0.91	51.4	85.3	60.7
		53.3	104	57.2	1.10	49.6	90.7	59.7
		53.5	105	49.2	0.84	51.9	89.3	60.7
		53.6	105	56.0	1.01	49.3	88.0	60.7
		54.0	106	49.3	0.91	52.5	89.3	60.0
		54.2	106	58.7	1.14	48.7	82.7	59.7
		54.9	107	50.4	0.97	52.8	89.3	61.3
		56.3	110	63.5	0.99	47.1	91.3	61.7
Noble		51.2	100	56.6	1.02	47.6	91.0	62.3
$L.S.D._{0.05}$		9.2		11.8	0.21	3.9	7.2	2.8

greater than Noble were selected from W2, W3, and C2. W3 and C2 also had lines 8 and 7% greater than Noble, respectively. Only one of the 11 lines selected from W populations had a SYD equal to Noble, whereas 15 of the 30 lines selected from the C populations had SYD's equal to or greater than Noble. The GR's of lines selected from W populations generally were lower than lines from C populations; only two selected lines from W populations compared to 13 from C populations had GR's equal to or greater than Noble. The HI's of all the lines selected from W populations were between 50 and 55%,

whereas selections from C populations ranged from 44 to 53%, with 17 of 49% or less. The highest GYD line had an HI of 54.6%. HT differences among selected lines were small and few lines deviated from the 87-91 cm range. One very short line was selected in each of W3 (80.7 cm) and C2 (82.7 cm). Most selected lines had HD's between 60-62 days, but three lines from W populations and two from C populations had HD's of 59 days.

Genetic Variation for GYD in Population C2

The genetic variance component for GYD in C2, a population containing germplasm from six A. sativa cultivars, was 19% less than the variance component in C1, a population containing germplasm from only three cultivars (Table 8). C2 was partitioned into three groups, A, B, and D, based on the single-cross combinations among Otter, Grundy, and Noble that constituted the first crosses in the development of this population (Table 39). The genetic variances in groups A and B were comparable to those found in W1, W2, W3, and C1, but the D group had a genetic variance 43-49% less than the other groups. Subsequent partitioning of the D group into subgroups based on the third parent, Lang (D1), Wright (D2), and Chief (D3), showed that D1 and D2 had variances equal to the overall D group, but D3 had a variance 50% less than D1 and D2. The ranges of the three subgroups were D1 (33.5 q/ha),

Table 39. The pedigrees, symbols, genetic variances and means for GYD, and inbreeding coefficients for the three 3-way cross combinations in C2, and 3-way crosses where Noble x Otter was the single cross

Pedigree	Symbol	Genetic variance	Inbreeding coefficient	Mean GYD
Otter x Grundy 2x Z[a]	A	44.3 ± 5.67	0.18	46.0 ± 0.54
Grundy x Noble 2x Z[a]	B	40.0 ± 5.27	0.27	48.1 ± 0.52
Noble x Otter 2x Z[a]	D	22.7 ± 3.64	0.20	49.1 ± 0.43
Noble x Otter 2x Lang	D1	22.4 ± 5.87	0.26	46.8 ± 0.72
Noble x Otter 2x Wright	D2	23.9 ± 6.93	0.07	51.6 ± 0.78
Noble x Otter 2x Chief	D3	11.9 ± 4.22	0.26	48.8 ± 0.60

[a]Z indicates 3-way crosses with Lang, Wright, and Chief.

D2 (27.1 q/ha), and D3 (23.3 q/ha). Differences in mean GYD's occurred among the groups and subgroups, but five, six, and seven agronomically superior lines were selected from groups A, B, and D, respectively. D1, D2, and D3 had five, zero, and two superior lines, respectively. Partitioning C1 into three groups based on 3-way crosses between Otter, Grundy, and Noble showed that the group with the parentage Noble x Otter 2 x Grundy had a genetic variance comparable to W1, W2, and W3. The estimated inbreeding coefficients of the 3-way F_1's, in C2, were not associated with the relative magnitudes of the genetic variances. Random F_1 seeds from crosses between Noble and Otter were chosen when the 3-way crosses with Lang, Wright, Chief, and Grundy were made.

Partitioning of Genotypic Variances in W Populations

Genetic variation among Bc_1 families for GYD was not significant in W1, W2, and W4, while in W3, 18% of the genetic variation was attributed to that source (Table 40). Variation among Bc_2 families accounted for 21-39% of the genetic variation, but variation among lines within Bc_2 families accounted for 61-69%. Similarly, 62-77% of the genetic variation for SYD was attributed to variation among lines within Bc_2 families, 23-38% to variation among Bc_2 families, and W4 was the only population where variation among Bc_1 families was significant (Table 41). W2 and W3 had 8 and

Table 40. Genetic variance components for GYD in W populations partitioned by backcross families

Source	W1	W2	W3	W4
Bc_1 families	ns[a]	ns	7.65	ns
Bc_2 families (Bc_1 families)	14.55	14.86	9.34	19.44
Within Bc_2 families (Bc_1 families)	32.52	29.24	26.61	30.09

[a]ns indicates component was not significant. All variance components listed were significant at the 1% level.

Table 41. Genetic variance components for SYD in W populations partitioned by backcross families

Source	W1	W2	W3	W4
Bc_1 families	ns[a]	ns	ns	8.41
Bc_2 families (Bc_1 families)	23.35	23.01	13.88	21.25
Within Bc_2 families (Bc_1 families)	51.22	38.24	45.71	52.58

[a]See footnote a, Table 40.

13% of the genetic variation for GR attributed to variation among Bc_1 families, 29-37% to Bc_2 families, and 56-67% to lines within Bc_2 families (Table 42). Similar results were found for HI, HT, and HD.

Table 42. Genetic variance components for GR in W populations partitioned by backcross families

Source	W1	W2	W3	W4
Bc_1 families	ns[a]	0.001	0.002	ns
Bc_2 families (Bc_1 families)	0.007	0.004	0.005	0.006
Within Bc_2 families (Bc_1 families)	0.012	0.009	0.009	0.012

[a]See footnote a, Table 40.

DISCUSSION

Population Means and Deviations

Elite lines released for commercial production are considered to be "finely-tuned" genotypes that combine new agronomic characteristics with traits already found in existing cultivars. The deviations of C population means from mid-parent values demonstrated that the gene action controlling this fine tuning in the cultivars used in this study was not entirely additive. Significant deviations for GYD, SYD, GR, and HT were all in the directions away from the desirable agronomic phenotype (Tables 6, 11, 16, 26). W populations were expected to contain a mean of 12.5% A. sterilis germplasm and were expected to have higher frequencies of deleterious linkages, which may have accounted for the large deviations in GYD and SYD in W1, W3, and W4, and in GR in W3 and W4 (Tables 6, 11, 16). Williams (1969) found negative and zero deviations in adapted x exotic (predominantly A. sativa lines) crosses, but zero and plus deviations in corresponding adapted x exotic 2x adapted crosses for GYD, SYD, and HT, possibly due to the restoration of favorable epistatic combinations present in the adapted parents. W populations had negative and larger deviations than C populations in spite of two backcrosses to adapted parents, suggesting there was a greater distortion of the genome through the

use of A. sterilis germplasm in this study than was found by Williams. Further, Lawrence and Frey (1976) concluded that additive and additive x additive epistatic gene effects and the break-up of repulsion-phase linkages accounted for the genetic variation for GYD in A. sativa-A. sterilis crosses and Leininger and Frey (1962) found epistatic gene effects for GYD and HD in crosses between adapted and unadapted A. sativa lines. However, W2 had deviations equal to or less than the C populations for GYD, SYD, and GR, which indicated that variation for specific combining ability in A. sativa-A. sterilis crosses could be found (Tables 6, 11, 16).

The evolution of multilocus coadapted gene complexes in plants and animals has been described (Wright, 1956; Grant, 1971; Ford, 1978), and Allard et al. (1972) found evidence of such complexes in wild populations of A. barbata. If variation for specific gene complexes is absent within sections of the A. sativa and A. sterilis gene pools, but variation exists between gene pools, then deviations would occur in progeny of hybrids between the two gene pools due to segregation at the coadapted loci.

The cytoplasmic differences between W1 and W2, and W3 and W4 did not result from reciprocal crosses; however, A. sterilis cytoplasm was associated with larger deviations for SYD and GR than was A. sativa cytoplasm (Tables 11, 16).

This also caused W1 and W2 to have large negative deviations for HI, because their SYD deviations were smaller than in other populations (Table 21). Robertson (1980) reported positive increments in GYD, SYD, HD, HT, and GR associated with A. sterilis cytoplasm in early backcross generations, but the advantage for SYD, HT, and GR disappeared by the Bc_2 generation. The results of this study did not indicate any clear advantage in the use of A. sterilis, rather than A. sativa, cytoplasm in an oat breeding program.

The magnitudes of the differences among population means for HD were small (Table 31). C2 was only one day later than the other five populations, but C and W populations differed in the sizes of their deviations due to the earlier mid-parent values in C populations. Whether the smaller deviations in W populations were due to the effects of A. sterilis germplasm or the break-up of additive x additive epistatic gene effects for earliness in the A. sativa genotypes was unclear.

In contrast to other plant vigor traits, the deviations for HT were positive, yet similar to other traits, in the direction away from the desired agronomic type (Table 26). There was no apparent association between deviations and germplasm source for this trait.

Variances

The smaller population means found in W populations due to the effects of A. sterilis germplasm were not unusual; however, the small genetic variances for GYD, SYD, and GR were unexpected (Tables 8, 13, 18). A. sterilis germplasm has been described as a source of variability for genes controlling GYD (Lawrence and Frey, 1975; Frey, 1976) and GR (Takeda and Frey, 1976; Helsel, 1980). In this study, W populations had genetic variances less than C populations for GR and SYD and equal to C1 for GYD. Further, examination of C1 and C2 indicated that it was the variance of C2 for GYD that was unusually small, rather than the variance of C1 that was unusually large (Table 39). A. sterilis germplasm did not substantially increase genetic variances for GYD, SYD, GR, or HI. It resulted in a slight increase in variance for HD (Table 33), resulting in more early lines (Table 32), and it increased genetic variance for HT, relative to C1, producing a higher frequency of tall lines (Tables 27, 28).

W populations were evaluated in the Bc_2, which was shown by Lawrence and Frey (1975) to be the first generation in interspecific oat crosses that was suitable for the recovery of transgressive segregates for complexly inherited traits. Further generations of backcrossing in the development of W populations probably would not have recovered substantially more transgressive segregates for GYD, SYD, or GR because the

genetic variances were already small, and W population means tended to be less than C population means. Previous studies found that genetic variation for GYD and SYD (Lawrence, 1974) and GR (Takeda and Frey, 1977) decreased after the Bc_2 generation without consistent changes in population means.

Failure to increase the genetic variation of several traits and simultaneously recover population means close to midparent values, in W populations, suggested that straight backcrossing may not be the most effective mating strategy in an A. sterilis introgression program. Backcrossing rapidly recovers the recurrent parent genotype and could limit recombination between chromosomes of the two species. Anderson (1939) found that actual recombinations in interspecific crosses were small fractions of the total possible under free assortment. Wall (1970) found that sib-mating in the Bc_1 generation, and a generation of selfing, both increased variation in Phaseolus interspecific hybrids. Lawrence and Frey (1976) and Takeda and Frey (1977) found that genes from A. sterilis were incorporated singly or in blocks into the A. sativa genome. In this study, variation among and within backcross families suggested that recombination between the two genomes, for genes controlling the traits measured, tended to be at random in the F_1 and Bc_1 generations (Tables 40, 41, 42). Isolated recombination of "super genes" did not contribute to genetic variation, and the results indicated that

the number of crosses in the backcrossing generations could be reduced, because the majority of the variation was expressed within Bc_2 families.

Transgressive Segregation

The development of W populations by backcrossing caused certain parents used as benchmarks in the identification of transgressive segregates to contribute unequally to the overall population. Thus, the frequencies of low transgressive segregates for GYD, SYD, GR, and high transgressive segregates for HD and HT in W populations would be small where the A. sterilis parent was the benchmark parent.

Lawrence and Frey (1975) found a mean of 14% of lines in the Bc_2 generation in eight matings were significantly greater than the recurrent parent for GYD, and Takeda and Frey (1977) found a mean of 8% in the same generation in 16 matings for GR. In this study, where the same adapted parent that contributed 50% of the germplasm to each population was the benchmark, the means were 1 and 3% for GYD and GR, respectively (Tables 9, 19). W populations had a higher percentage of early transgressive segregates and similar percentages of short transgressive segregates as C populations (Tables 29, 34). Lawrence (1974) found means of 15 and 7% transgressive segregates, in comparison to 4 and 5% in this study for HD and HT. However, the low parents in this study only

contributed 12.5 to 25% of the germplasm to the populations.

Unlike the previous introgression studies in oats, where a single recurrent parent was utilized throughout the backcrossing program, in this study, three different A. sativa parents were used with the objective of achieving favorable recombinations within and between the two germplasms. However, if the frequencies of favorable recombinations in C1 was, say, x, and in a single parent recurrent backcross program, also x, a crude approximation of the frequency of favorable recombinations within and between the two germplasms was x^2. Favorable recombinations of one type could have been masked by inferior recombinations of the other type.

Correlations Among Traits

GYD is the product of GR x growth duration x HI. In Iowa, growth duration is limited to approximately 100 days, and as a consequence of the curvilinear relationship between GYD and HI, optimum HI values lie between 42-48% (Takeda and Frey (1976). Thus, the route to increased GYD should be through GR. Genotypic correlations between GYD and GR of 0.7-0.9 and between GYD and HI of 0.1-0.4 (Table 10) were similar to those reported by Takeda and Frey (1976, 1977) and Takeda et al. (1979, 1980). A multiple regression analysis of GYD on HI and GR indicated that GR and HI accounted for most of the variation in GYD, and GR was more important than

HI, as previously reported by Takeda and Frey (1976) and Takeda et al. (1979). Nevertheless, GYD increases would be difficult to achieve through GR if GR and HI were strongly negatively correlated. In interspecific (Takeda and Frey, 1977) and intraspecific (Takeda et al., 1979) crosses in oats, independence between these traits was observed, but Takeda et al. (1980) reported a moderately negative relationship in progeny of intraspecific crosses advanced in bulk for nine generations. In this study, genotypic correlations between GR and HI were slight to moderately negative (-0.2 to -0.5) in W populations, and highly negative (-0.6 to -0.7) in C populations (Table 20).

Differences in genetic variances and population means indicated that selection in C, rather than W, populations would result in greater gains in GR (Tables 16, 18). High GR lines in W populations had larger HI's than in C populations due to smaller SYD's (Table 36), and lines selected on the basis of overall agronomic quality in W populations had high HI's (Table 38). However, a line with high GYD and HI, but poor SYD, would be prone to lodging, and SYD is an important product of oat production. Hybrids between selected high GYD lines from the two sets of populations would determine if A. sterilis is a new source of variability for HI and whether high GYD, SYD, and HI can be combined in a single genotype. Robertson (1980) reported high HI associated with

high GYD in lines with A. sterilis cytoplasm.

The results of this study were less encouraging with regard to the short-term value of utilizing A. sterilis germplasm in oat breeding programs than reported previously (Lawrence and Frey, 1975, 1976; Takeda and Frey, 1977). The results indicated that the greatest short-term gains would be achieved by selection in C populations, i.e., populations developed by intraspecific hybridization. Lines selected from these populations had better overall agronomic quality than lines selected from W populations. Although the line with the highest GYD, selected for overall agronomic quality, came from W3, its value would be as a parent in initiating a second cycle of breeding. The present method utilized at the Iowa Agriculture and Home Economics Experiment Station of introgressing small amounts of A. sterilis germplasm into the A. sativa gene pool through backcrossing, followed by another cycle of breeding to exploit new variation associated with wild germplasm, has been endorsed by these results. The exploitation of A. sterilis germplasm is a long-term project restricted by our inability to identify specific superior combinations of adapted and exotic lines.

SUMMARY

Six oat populations developed by interspecific (A. sterilis x A. sativa) and intraspecific (A. sativa x A. sativa) hybridizations were compared to evaluate their potential utility in an oat breeding program. Four interspecific (W) populations of 512 lines each, with a mean of 12.5% A. sterilis and 87.5% A. sativa germplasm, were compared to two intraspecific (C) populations of 510 and 576 lines, developed by intercrossing superior A. sativa cultivars.

W population means tended to be smaller than C population means for GYD, SYD, and GR, similar for HI and HD, and larger for HT. Deviations of observed from expected means tended to be larger in W than C populations for GYD, SYD, and GR, which implied that deleterious linkages and/or non-additive gene effects were more important in W than C populations for these traits. The results did not reveal any clear advantage in the use of A. sterilis over A. sativa cytoplasm in an oat breeding program.

Avena sterilis germplasm did not substantially increase genetic variances for GYD, SYD, GR, or HI, but tended to increase the variance of HD and HT. Genotype x location variances were generally significant for GYD, SYD, and HI, but were small in magnitude in comparison to genetic variances.

C populations had more high transgressive segregates for GYD, SYD, and GR, but W populations had more low transgressive

segregates for HD. Lines selected on the basis of GYD from C populations had larger SYD's, GR's, and later HD's. C populations had higher frequencies of agronomically desirable lines and lines selected from W populations tended to have lower SYD's and larger HI's. The highest yielding line selected on the basis of agronomic quality came from W3.

Genotypic correlations between GR and HI were larger than previously reported for progeny from interspecific oat matings, and there was a stronger association between GYD and HI in W than C populations.

The results indicated that the greatest short-term gains would be achieved by selection in C populations. The exploitation of A. sterilis germplasm is a long-term project; thus, lines with high GYD and good agronomic quality, selected from W populations, can be used as parents to initiate a second cycle of breeding. In this manner, any new genetic variability transferred from the A. sterilis parents can be utilized while simultaneously improving the overall agronomic quality of the lines selected from W populations.

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